



Evaluation of predicted ration nutritional values by NRC (2001) and INRA (2018) feed evaluation systems, and implications for the prediction of milk response

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ABSTRACT

Net energy and protein systems (hereafter called feed evaluation systems) offer the possibility to formulate rations by matching feed values (e.g., net energy and metabolizable protein) with animal requirements. The accuracy and precision of this approach relies heavily on the quantification of various animal digestive and metabolic responses to dietary changes. Therefore, the aims of the current study were, first, to evaluate the predicted responses to dietary changes of total-tract digestibility (including organic matter, crude protein, and neutral detergent fiber) and nitrogen (N) flows at the duodenum (including microbial N and undigested feed N together with endogenous N) against measurements from published studies by 2 different feed evaluation systems. These feed evaluation systems were the recently updated Institut National de la Recherche Agronomique (INRA, 2018) and the older, yet widely used, National Research Council (NRC, 2001) system. The second objective was to estimate the accuracy and precision of predicting milk yield responses based on values of net energy (NE_L) and metabolizable protein (MP) supply predicted by the 2 feed evaluation systems. For this, published studies, with experimentally induced changes in either NE_L or MP content, were used to calibrate the relationship of NE_L and MP supply, with milk component yields. Based on the slope, root mean square prediction error, and concordance correlation coefficient (CCC), the results obtained show that total nonammonia nitrogen flow at the duodenum was predicted with similar accuracy and precision, but considerably better prediction was achieved when the INRA model was used to predict organic matter and neutral detergent fiber digestibility responses. The average NE_L and MP content predicted by both models

was similar, but NE_L and MP content of individual diets differed substantially between both models as indicated by determination coefficients of 0.45 (NE_L content) and 0.50 (MP content). Despite these differences, this work shows that when response equations are calibrated with NE_L and MP values either from the INRA model or from the NRC model, the accuracy and precision (slope, root mean square prediction error, and CCC) of the predicted milk component yields responses is similar between the models. The lowest accuracy and precision were observed for milk fat yield response, with CCC values in the range of 0.37 to 0.40, compared with milk lactose and protein yields responses for which CCC values were in the range of 0.75 to 0.81.

Key words: digestibility, duodenal flow, model evaluation, milk responses

INTRODUCTION

Numerous feed evaluation systems for dairy cows have been developed and are regularly being updated to incorporate recent knowledge, among which are the National Research Council (NRC, 2001), Cornell Net Carbohydrate and Protein System (CNCPS; Fox et al., 2004; Van Amburgh et al., 2015), DVE/OEB system (Tamminga et al., 1994; Van Duinkerken et al., 2011), NorFor (Volden, 2011), and Institut National de la Recherche Agronomique (INRA, 2018). All these systems offer the possibility to formulate rations by matching nutrient supply with animal requirements. The validity of using such an approach relies heavily on the relationship between the feed values and the animal performance in terms of milk yield, milk composition, and body changes. In other words, it implies that these systems must adequately predict animal responses to dietary changes. For the prediction of milk responses to dietary changes, 2 important aspects are (1) accurate estimation of nutrients available for absorption and (2) accurate estimation of nutrient partitioning and efficiency of utilization of those absorbed nutrients

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into milk (Oldham and Emmans, 1989; Dijkstra et al., 2007). With regard to the first aspect, MP and NE_L are often used to characterize the overall nutritive value of a ration. Although it is recognized that the use of NE_L has limitations for the prediction of milk energy yield and milk fat yield (van Knegsel et al., 2007a,b; Boerman et al., 2015), and similarly that MP has limitations to predict milk protein yield (Lapierre et al., 2012; Nichols et al., 2019), NE_L combined with MP has proven to be a useful estimator of milk component yields (Huhtanen and Hristov, 2009; Daniel et al., 2016, 2017). In this context, it is important to evaluate the accuracy and precision of MP and NE_L values predicted by different feed evaluation systems. Unfortunately, direct phenotypical measurement against which MP and NE_L can be compared are lacking. A possibility for evaluating the quality of these nutritional values is to compare underlying elements, as predicted by each feeding system, with biological parameters for which numerous measurements have been made and are published in the literature. Examples of such underlying elements are total-tract digestibility of OM, required to obtain NE_L , and flows of N measured at the duodenum, required to obtain MP. Therefore, the comparison of measured total-tract digestibility (including OM, CP, and NDF) and measured N flows at the duodenum (including microbial N and undigested feed N, together with endogenous N) with their predictions by the feed evaluation systems represents the first objective of the present study. A large data set from published studies was used for that purpose. For conciseness and clarity of reporting, we limited the comparison to 2 feeding systems: the recently updated INRA (2018) with the older, yet widely used, NRC (2001) system. The second objective was to estimate the accuracy and precision of predicting milk responses based on values of NE_L and MP supply predicted by these 2 feed evaluation systems. For this, a large data set from the literature (Daniel et al., 2016) with experimentally induced changes in either NE_L or MP content, was used to calibrate the relationship of NE_L and MP supply with milk component yields for both feed evaluation systems.

MATERIALS AND METHODS

Total-Tract Digestibility and Duodenal N Flows

Data Set. The data set used in a previous meta-analysis for quantification of milk responses to dietary changes (Daniel et al., 2016) was reused for the purpose of the present publication. This data set consisted of 168 published scientific papers from which treatments (825 in total) focused on the effect of changes in dietary

energy or protein content (or both) on milk yield and composition. The full description of this data set is described by Daniel et al. (2016). Collected data that were excluded from the previous analysis of Daniel et al. (2016) because the experimental design was not related to NE_L or MP change, were now re-considered for the purpose of evaluating the ability of the NRC (2001) and INRA (2018) feed evaluation systems to predict total-tract digestibility and N flow at the duodenum. From the 491 treatment means that were initially discarded, 285 had either total-tract digestibility of OM, CP, and NDF, or N flow at the duodenum reported. All these 285 treatment means had the ration composition described in term of ingredients (% DM of the total diet) as well as dietary CP content (g/kg of DM), DMI (kg/d), and BW (kg) reported. Therefore, the final data set used for the current study consisted of 1,110 treatment means (229 published manuscripts, full list in Supplemental File S1, <https://doi.org/10.3168/jds.2020-18286>). Among these treatments, 229, 255, and 161 had measured N flows at the duodenum for total NAN, microbial N (MN), and nonammonia, nonmicrobial N (NANMN, i.e., rumen bypass feed N plus endogenous N), respectively. Digestibility of OM, CP, and NDF was measured in 761, 637, and 684 treatments, respectively.

Calculations of Digestibility and Duodenal N Flows. The digestibility of the organic matter (OMD), of the crude protein (CPD), and of the NDF (NDFD), as well as all N flows at the duodenum (NAN, MN, and NANMN), NE_L , and MP values, were estimated using the INRA (2018) and NRC (2001) feed evaluation systems. The method used to estimate nutrient supply with INRA (2018) was summarized in Daniel et al. (2016) and described in Sauvant and Nozière (2016) and INRA (2018). For the NRC, the equations listed in the NRC (2001) publication were used to reconstruct the model to estimate nutrient supply. Predicted chemical composition for the ingredients, for which nutritional values were calculated in the 2 feed evaluation systems, were derived from the same feed library (Baumont et al., 2007), and details of this selection are given in Daniel et al. (2016). In brief, chemical composition of feed ingredients with analysis reported in manuscripts were matched by selecting feed ingredient or combination of feed ingredients that would minimize difference between predicted and analyzed chemical composition. If several codes were available for one ingredient (e.g., forages, soybean meal) and no analysis was reported for that ingredient, the code was chosen to minimize the differences between the estimated and measured CP, NDF, and starch of the total diet. Between predicted and reported chemical composition, the slopes (unad-

justed for effect of experiment) were 0.98, 0.86, 0.99, and 0.98 and root mean square errors (**RMSE**) were 7, 30, 20, and 30 g/kg of DM for CP, NDF, forage NDF, and starch, respectively. Slopes did not differ from 1 ($P > 0.10$) except for NDF ($P < 0.01$). Using the same chemical composition as inputs for both models was necessary to allow a strict comparison of the systems (equations, rumen degradability parameters), and not of the feed tables (choice of ingredients and their composition). Nevertheless, some chemical values were required for the NRC model but not present in the INRA feed library. This is, for example, the case for NDIN and ADIN. In these cases, these values were retrieved from the NRC feed library by matching the ingredient with the closest characteristics (i.e., ingredient type, chemical composition). Additionally, the NRC feed library was also used to select feed values related to digestive process, and therefore specific to the model to be evaluated, such as kd, A, B, and C protein fraction, and RUP digestibility.

Statistical Analysis. Statistical analyses were carried out using PROC MIXED of SAS 9.4 (SAS Institute Inc., Cary, NC). The first objective was to compare the measured N flows at the duodenum and total-tract digestibility with their predicted values for each of the 2 feed evaluation systems investigated (NRC, 2001; INRA, 2018). The model used for that purpose was

$$Y_{ij} = \mu + S_i + \beta \times X_{ij} + \varepsilon_{ij}, \quad [1]$$

where Y_{ij} is the measured N flow at the duodenum (for NAN, MN, or NANMN) or measured total-tract digestibility (for either OM, CP, or NDF) for experiment i and treatment j , and X_{ij} is the respective prediction made by the NRC (2001) or INRA (2018) feed evaluation system. As the objective was to evaluate the ability of both feed evaluation systems to predict responses of N flows at the duodenum and total-tract digestibility to dietary changes, and not absolute values per se, the comparison with measured values was adjusted for the fixed effect of experiment (S_i) on the intercept μ only. Because of this focus on the slope (i.e., the response), we have preferred to use a fixed effect instead of a random effect to adjust for the effect of experiments here and throughout this manuscript, because a fixed effect keeps the variation of slopes between experiments unchanged. In theory, such adjustment may limit the applicability of the equations; however, we have previously seen (using the same data set) that the choice of using fixed or random to adjust for the effect of study has very negligible effect on the estimates and SE of the slopes (Daniel et al., 2016). Finally, μ is the intercept of the equation, β is the linear coefficient relating Y_{ij}

with X_{ij} , and ε_{ij} is the random residual for experiment i and treatment j . With this model, Y values adjusted for the experiment effect were generated as described in St-Pierre (2001). Briefly, these adjusted Y values are the result of the addition of obtained residual to its corresponding Y predicted value. The adjusted Y values were then used to evaluate the quality of the independent predictions (i.e., flows or digestibilities predicted by NRC and INRA), using the concordance correlation coefficient (**CCC**) and its components (r and C_b , measurement of precision and accuracy, respectively), calculated as described in Lin (1989), and the root mean square prediction error (**RMSPE**) computed as previously described (Theil, 1966; Bibby and Toutenburg, 1977). The RMSPE was decomposed into error due to overall bias, error due to deviation of the regression slope from unity, and error due to disturbance (random error; Bibby and Toutenburg, 1977).

Milk Responses to Changes in NE_L and MP Supply

Data Set. The second objective was to quantify, within the experiment, responses in milk energy yield, total protein yield (i.e., the sum of the exported protein, see Supplemental File S2 for details, <https://doi.org/10.3168/jds.2020-18286>), and milk component yield (for fat, protein, and lactose) to changes in NE_L and MP supply, as predicted by each of the 2 feed evaluation systems. The data used for this objective were identical as in Daniel et al. (2016). Briefly, the data contain 282 experiments (but only 178 for milk lactose yield) with a total of 825 treatment means (545 for milk lactose yield) focused on the changes in dietary energy, protein content, or both.

Calculations and Statistical Analyses. To answer this second objective, the simplest approach is to use NE_L and MP supply as independent variables. However, a major limitation with this approach is that the range of NE_L and MP supplies differ between experiments. This would induce confounding effects between these supplies and the effect of experiment (Daniel, 2016). Adjusting the regression for the effect of experiment does not entirely solve this issue as it only adjusts experiments vertically (based on milk yield for example) but not horizontally (based on NE_L and MP supply). Therefore, to avoid such confounding effects, NE_L and MP supply were centered, following the same methods used in Daniel et al. (2016). This approach aims to express NE_L and MP supply relative to meaningful reference supplies, chosen to be the supply of MP and NE_L for lactation (i.e., MP and NE_L supply above maintenance) at which MP efficiency for milk protein is 0.67 (reference in NRC, 2001 and INRA, 2018) and

NE_L efficiency for milk energy is 1.00 (equivalent to a zero net energy balance). To achieve this, first the slope (α) of the linear relation between MP supply for lactation (S_{ij}) and MP efficiency (F_{ij}) was determined (with experiments fitted as a fixed effect). Then the centered MP supply for lactation ($= \Delta\text{MP67}$, kg/d) was calculated as

$$\Delta\text{MP67} = S_{ij} - S_i + \alpha(F_i - 0.67), \quad [2]$$

where S_i is the experiment mean MP supply for lactation and F_i is the experiment mean MP efficiency. Similarly, the centered NE_L supply for lactation ($= \Delta\text{NE}_{L100}$, MJ/d) was calculated as

$$\Delta\text{NE}_{L100} = S_{ij} - S_i + \alpha(F_i - 1.00), \quad [3]$$

where S_i is the experiment mean NE_L supply for lactation, F_i is the experiment mean NE_L efficiency, and α is the slope of the linear relation between NE_L supply for lactation (S_{ij}) and NE_L efficiency (F_{ij}). It should be noted that this adjustment maintains the within-experiment relationships intact (e.g., NE_L and MP supply), it only reorganized the experiments based on observed MP and NE_L efficiency (e.g., experiments with high efficiencies will have lower ΔMP67 and ΔNE_{L100} than experiments with low efficiency). Equations used to calculate MP and NE_L efficiency are presented in Supplemental File S2 (<https://doi.org/10.3168/jds.2020-18286>), and obtained coefficients α as well as an example of the adjustment presented above can be found in Supplemental File S3 (<https://doi.org/10.3168/jds.2020-18286>).

Finally, responses were estimated with the following model, using the data set (825 treatments, 282 experiments; except for milk lactose yield: 545 treatments, 282 experiments) that was selected and coded for that purpose (see Daniel et al., 2016):

$$Y_{ij} = \mu + S_i + e1 \times \Delta\text{NE}_{L100} + p1 \times \Delta\text{MP67} + e2 \times \Delta\text{NE}_{L100}^2 + p2 \times \Delta\text{MP67}^2 + a \times \Delta\text{MP67} \times \Delta\text{NE}_{L100} + \varepsilon_{ij}, \quad [4]$$

where Y_{ij} is the milk energy yield, total protein yield, or milk component yields for experiment i and treatment j . The parameter μ is the centered intercept that represents the mean value of the Y variable when MP efficiency is 0.67 and NE_L efficiency is 1.00; S_i is the fixed effect of experiment i , $e1$ and $e2$ are the linear and quadratic coefficients of ΔNE_{L100} ; $p1$ and $p2$ are the coefficients for the linear and quadratic effects of ΔMP67 ; a is the coefficient adjusting the response slope

for the interaction between ΔMP67 and ΔNE_{L100} ; and ε_{ij} is the random residual for experiment i and treatment j . Corrected Akaike's information criterion (**AICc**) was used to select the best model, with non-significant terms being progressively dropped. Differences in AICc greater than 3 between 2 models indicate that there is good evidence that the model with the smaller AICc better describes the data than the model with the larger AICc (Burnham and Anderson, 2002). Observations from model [4] were considered as outliers when their studentized residuals were higher than 3 (Sauvant et al., 2008). In this case, they were removed stepwise until there were no such outliers left. For each analysis, the number of outliers removed are reported in Supplemental File S4 (<https://doi.org/10.3168/jds.2020-18286>), together with the RMSE. As the RMSE is influenced by the number of outliers removed, it could not be used to fairly compare the response equations fitted for each of the 2 feed evaluation systems. Furthermore, in practice, when milk component yields and the details of the ration fed are known, one would like to use these response equations to predict milk response to a nutritional change from the initial ration. Therefore, to mimic this scenario, and circumvent the problem of inappropriate RMSE comparison, one treatment of each experiment (178 for lactose, 282 for other variables) was randomly selected and used as inputs. Under these circumstances, the challenge is to estimate where the group of cows is on the response curves (see Daniel et al., 2017 for further details on this aspect). A possible approach is to use response equations obtained for milk energy yield and total protein yield, with model [4], to estimate the intercept μ . These intercepts or pivot μ give the total protein yield (i.e., $0.67 \times \text{MP supply}$) and milk energy yield (i.e., $1.00 \times \text{NE}_{L100}$) at which MP efficiency is 0.67 and NE_L efficiency is 1.00. Provided that this pivot can be calculated using inputs from the selected treatment, it is then possible to apply all response equations obtained with model [4] to predict milk yield and milk component yields of other treatments for each experiment (Y_{ij}). Full details of the methods used to estimate the pivot can be found in Supplemental File S5 (<https://doi.org/10.3168/jds.2020-18286>). The calculated pivots were then used together with the milk component yield response equations to predict milk component yields for the other treatments in the experiment, as exemplified in Supplemental File S5. Finally, the quality of the prediction (including treatments considered previously to be outliers, excluding the treatment used to calculate the pivots) was assessed through the RMSPE, its decomposition to error due to overall bias, error due to deviation of the regression slope from unity, error due

to disturbance, CCC, and its components (r and C_b), as described above. Therefore, a total of 543 treatment means ($= 825 - 282$) were used for the evaluation of milk energy yield, milk fat yield, and milk protein yield. For milk lactose yield, this total was 367 treatment means ($= 545 - 178$). Although we refer to predicted values for milk responses, it is important to note that these predictions were entirely made on the calibration data set. Therefore, the accuracy and precision of these predictions only reflect the ability of each system of equations to describe observed milk responses in a large data set (a total of 282 experiments) that covered a wide range of diet characteristics and therefore a large part of the plausible ranges of NE_L and MP supplies that can be expected in practical situations.

RESULTS AND DISCUSSION

Prediction of Digestibility and N Flow at the Duodenum

Results of the comparison between predicted and observed responses in digestibility and N flows at the duodenum for the 2 models are shown in Table 1, and illustrations of the prediction quality are shown in Figures 1 and 2. It is important to consider that, because the main interest of this evaluation was to assess the ability of each of the 2 feed evaluation systems to predict responses in nutrient digestibility and N flows at the duodenum to dietary changes, all observed values were adjusted for the effect of the experiment (unadjusted values presented in Tables and Figures from Supplemental File S6, <https://doi.org/10.3168/jds.2020-18286>). Through this adjustment the focus is at the within-experiment variation, that is, the differences observed between 2 treatments of the same experiment. Thus, the closer the slope between observed and predicted values is to 1, the better the system is at capturing this within-experiment variability. Despite this adjustment, the other elements of statistics compiled (RMSPE and CCC) are not strictly reflective of the quality of the response but are also influenced by an overall under- and overprediction. An example of this can be seen in the prediction of CP digestibility where higher RMSPE and lower CCC were obtained with the NRC model despite a better slope (0.78 vs. 0.66, slopes different from 1, $P < 0.05$). In this case, the low quality of fit does not necessarily reflect a poor ability of the system to predict CP digestibility response but instead may reflect the overprediction of CP digestibility with the NRC model (Figure 1; 72.0% of error due to mean bias). Therefore, interpretation of the quality of the prediction response can only be made when the slope is considered together with measures of accuracy and

precision (RMSPE and CCC). Considering this, OM and NDF digestibility were better predicted by the INRA model (Figure 1 and Table 1). In particular, the response in OM digestibility, a key determinant of the NE_L value of the ration, was predicted with a slope of 0.86 and a CCC of 0.75 by the INRA model, whereas these were 0.32 and 0.20 with NRC, respectively (all slopes different from 1, $P < 0.05$). A previous evaluation of the NRC model at predicting total-tract NDF and CP digestibility (White et al., 2017b) indicated the model underpredicted NDF digestibility by 16% (kg of NDF/d) and overpredicted true N digestibility (g of N/d) by 7%. Our evaluation conducted after adjusting for the effect of experiment, shows a very similar trend for apparent total-tract CP digestibility (%), with a 6.1% overprediction. Apparent total-tract NDF digestibility (%) was also underpredicted (mean bias of 36.8%) but by 8% only.

As observed in Figure 2 and indicated by the slope between observed and predicted values, the response of rumen bypass N flow (NANMN) to dietary change was better predicted with the NRC model (slope 1.07 vs. 0.69, respectively), whereas the response of MN flow was better predicted with the INRA model (slope 1.29 vs. 0.31, respectively). However, these interpretations were not supported by the RMSPE and CCC, and this was mainly due to mean bias. Indeed, the MN flow for the INRA model and the NANMN flow for the NRC model were both underpredicted, by 11% and 9%, respectively. Previous works that have evaluated NRC prediction of postruminal N flows have shown contrasting outcome. For instance, Bateman et al. (2005) showed NANMN was underestimated by 43.7%, whereas White et al. (2017a) found this fraction was overestimated by 18%. Similarly, Bateman et al. (2005) found NRC (2001) model overestimates microbial N by 14.5%, in contrast to White et al. (2017a) who found an underprediction of 14.5%. Such discrepancies between studies may be explained by the very large contribution of the study effect (e.g., in the NRC model 90% of the total variance for MN was explained by the study effect). As our work aimed to focus at the within-study effect, it is more interesting to contrast our results with studies that have adjusted for the study effect. The low slope we found between observed and predicted MN by the NRC model (0.31 ± 0.07) is very different from what Broderick et al. (2010) found (1.26). Part of this difference is explained by the way MN was evaluated. In the current paper, we left out the effect DMI, by expressing MN per kilogram of DM, whereas Broderick et al. (2010) evaluated daily MN flow (in g/d). When we evaluated the prediction of MN by the NRC model (in g/d), we found a much higher slope of 0.75 ($\pm$ SE of 0.10), albeit lower than what Broderick et al. (2010)

Table 1. Summary of observed versus predicted digestibility (OM, NDF, and CP) and N flows at the duodenum for the 2 feed evaluation systems: NRC (2001) and INRA (2018), and within-experiment relationships were used to compute the statistics

Item	Model	N	Observed ¹	Predicted ¹	RMSPE ² (%)	ECT ³ (%)	ER ⁴ (%)	ED ⁵ (%)	r ⁶	C _b ⁷	CCC ⁸	Slope ⁹ (SE)
Apparent total-tract digestibility (%)												
OM	NRC	761	68.7 ± 2.2	65.6 ± 2.6	6.0	56.5	18.4	25.1	0.37	0.54	0.20	0.32 (0.03)
	INRA	761	68.7 ± 2.9	67.9 ± 2.7	3.0	17.4	3.2	79.4	0.79	0.95	0.75	0.86 (0.02)
NDF	NRC	684	49.7 ± 4.0	45.7 ± 4.5	13.1	36.8	28.7	34.5	0.26	0.69	0.18	0.23 (0.11)
	INRA	684	50.1 ± 5.8	47.6 ± 8.4	11.9	17.3	43.4	39.3	0.77	0.88	0.68	0.53 (0.02)
CP	NRC	637	66.7 ± 3.7	70.8 ± 3.6	7.1	72.0	2.7	25.3	0.76	0.62	0.47	0.78 (0.07)
	INRA	637	66.7 ± 3.7	69.3 ± 4.4	5.7	49.4	15.3	35.3	0.79	0.81	0.64	0.66 (0.02)
N flow at the duodenum (g of N/kg of DM)												
NAN ¹⁰	NRC	229	24.9 ± 2.1	24.3 ± 2.2	6.4	14.4	15.6	70.0	0.77	0.96	0.74	0.72 (0.04)
	INRA	229	24.9 ± 2.1	24.1 ± 2.1	6.6	23.5	9.5	67.0	0.77	0.93	0.72	0.76 (0.04)
NANMN ¹⁰	NRC	161	12.2 ± 2.2	11.1 ± 1.7	12.8	48.1	0.7	51.3	0.86	0.85	0.73	1.07 (0.05)
	INRA	161	12.1 ± 1.9	12.2 ± 2.1	11.6	0.6	21.2	78.2	0.76	0.99	0.75	0.69 (0.05)
MN ¹⁰	NRC	255	13.5 ± 1.0	13.4 ± 0.9	8.8	0.2	30.0	69.8	0.28	0.99	0.27	0.31 (0.07)
	INRA	255	13.5 ± 1.2	12.0 ± 0.5	13.1	68.7	0.7	30.5	0.57	0.32	0.18	1.29 (0.12)

¹Mean ± SD. The observed is the value obtained after adjusting for the effect of experiment plus the residuals of the model.²Root mean square prediction error expressed as a percentage of the observed mean.³Error due to intercept bias, as a percentage of total RMSPE.⁴Error due to slope bias, as a percentage of total RMSPE.⁵Error due to disturbance, as a percentage of total RMSPE.⁶Pearson correlation coefficient, which gives a measure of precision.⁷Bias correction factor, which gives a measure of accuracy.⁸Concordance correlation coefficient (scale from -1 to 1); CCC = $r \times C_b$.⁹Slope of predicted versus observed regression as determined in PROC REG (SAS Institute Inc., Cary, NC). All slope coefficients were different from 1 ($P < 0.05$) except for NANMN of NRC ($P = 0.15$).¹⁰NAN = nonammonia N; NANMN = nonammonia nonmicrobial N; MN = microbial N.

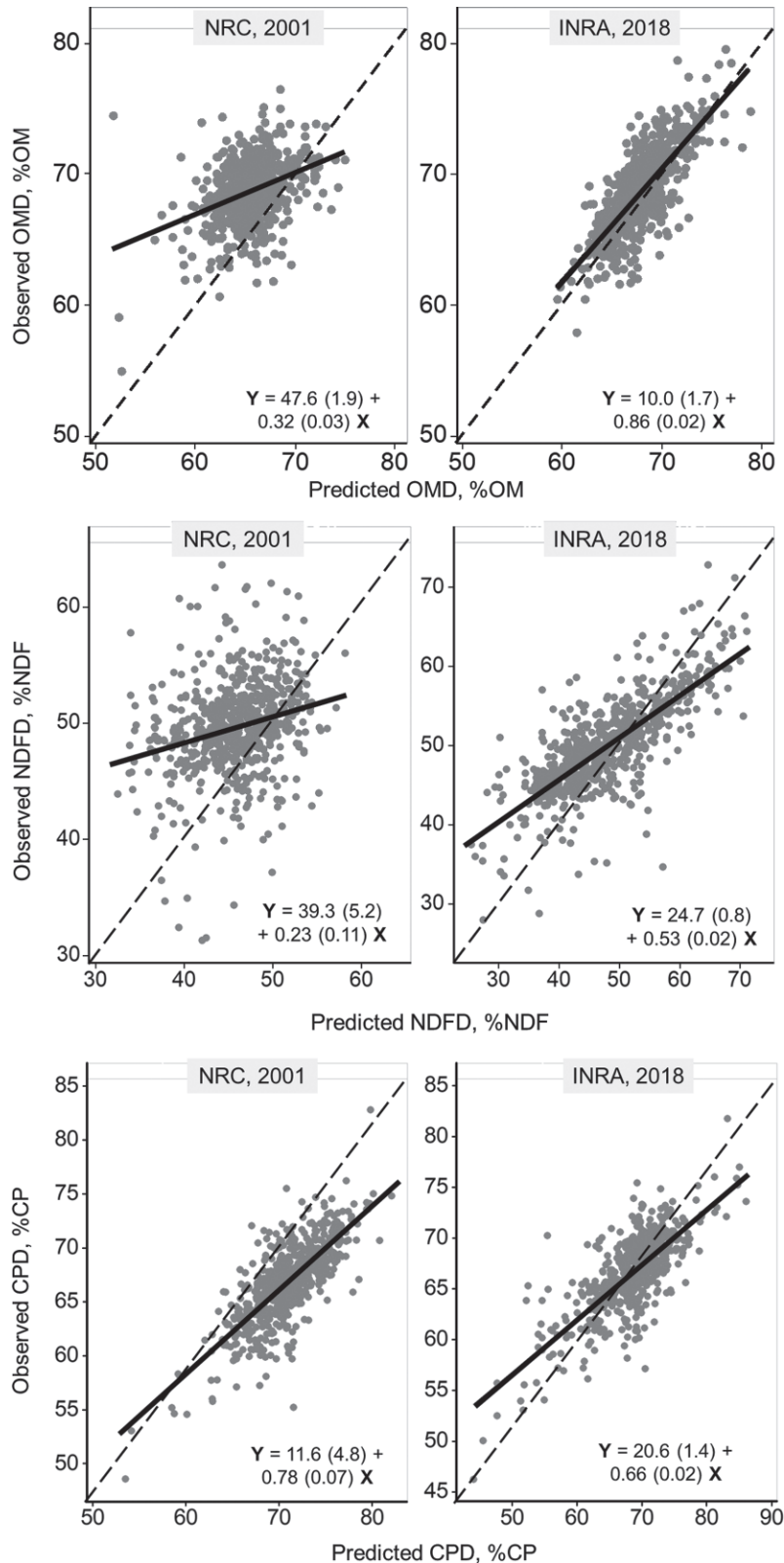


Figure 1. Comparison between observed values of apparent total-tract digestibility (digestibility of OM, OMD; digestibility of NDF, NDFD; and digestibility of CP, CPD) and values predicted by NRC (2001) and INRA (2018). The observed values were adjusted for the effect of experiment, as illustrated in St-Pierre (2001), to reflect the ability of each system to predict changes in digestibility within the experiment. The dashed line represents the line of unity; the solid line represents the regression line. The SE of the intercept and slope are shown in parentheses.

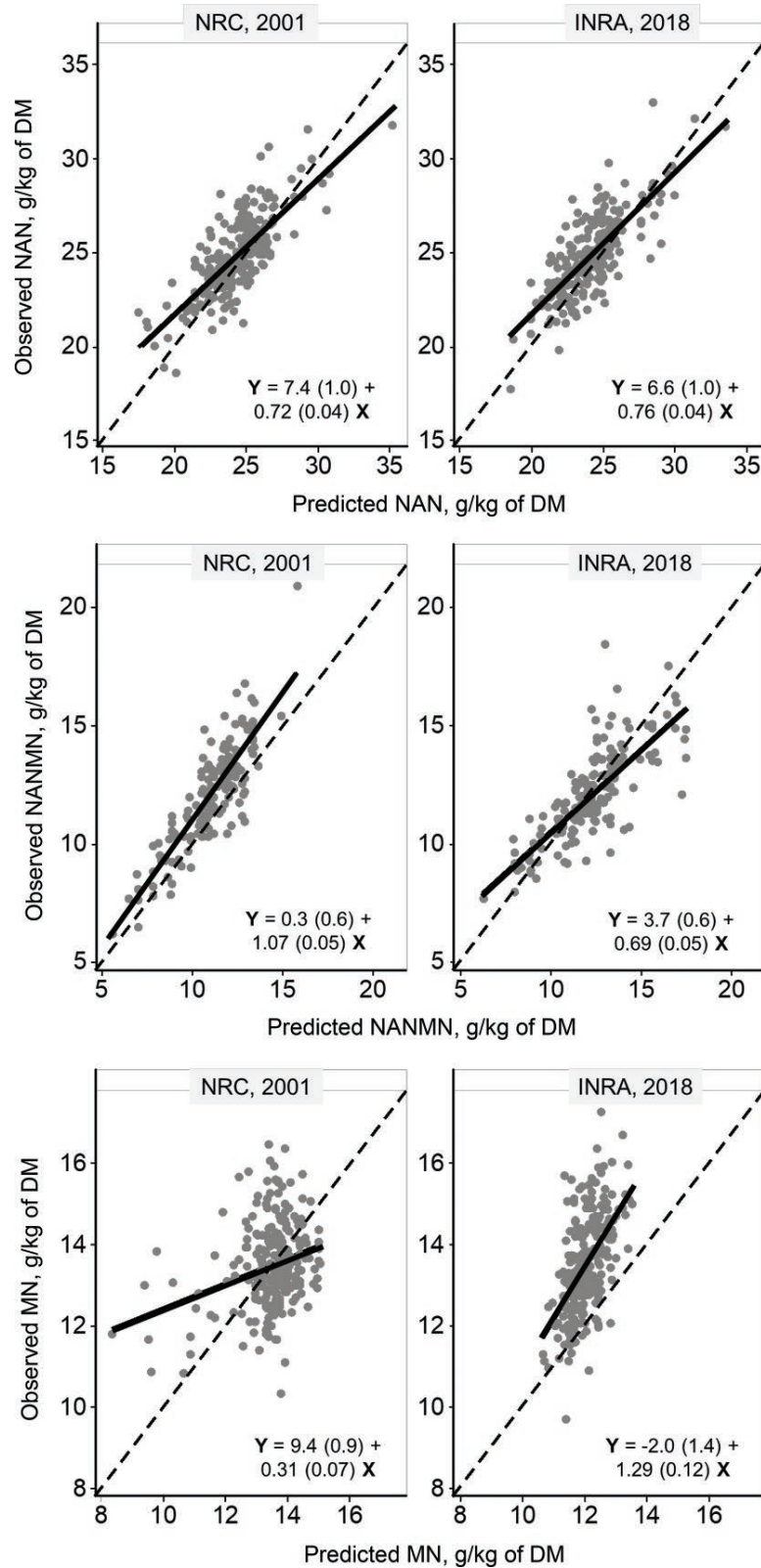


Figure 2. Comparison between observed values of N flows at the duodenum and values predicted by NRC (2001) and INRA (2018). The observed values were adjusted for the effect of experiment, as illustrated in St-Pierre (2001), to reflect the ability of each system to predict changes in digestibility within the experiment. The dashed line represents the line of unity; the solid line represents the regression line. MN = microbial nitrogen, NANMN = nonammonia, nonmicrobial nitrogen. The SE of the intercept and slope are shown in parentheses.

Table 2. Chemical composition for dietary treatments of the data set and calculated nutritional values with NRC (2001) and INRA (2018) feed evaluation systems¹

Variable	Nt	Mean	SD	Q1	Q3
Analyzed chemical composition (g/kg of DM)					
CP	1,110	171	22	158	183
NDF	1,073	343	56	302	377
Starch	566	241	94	181	302
EE	334	44	14	34	51
Calculated chemical composition (g/kg of DM)					
CP	1,110	170	21	158	182
NDF	1,110	343	58	303	377
Forage NDF	1,110	248	65	204	284
Starch	1,110	242	89	190	304
EE	1,110	42	14	32	49
Nutritional value calculated with NRC (2001)					
DE (MJ/kg of DM)	1,110	12.3	0.4	12.1	12.6
ME (MJ/kg of DM)	1,110	10.6	0.5	10.4	10.9
NE _L (MJ/kg of DM)	1,110	6.7	0.4	6.5	6.9
RDP (g/kg of DM)	1,110	114	17	104	123
RUP (g/kg of DM)	1,110	56	12	49	63
MP (g/kg of DM)	1,110	104	12	96	111
Nutritional value calculated with INRA (2018)					
DE (MJ/kg of DM)	1,110	12.1	0.6	11.7	12.5
ME (MJ/kg of DM)	1,110	10.6	0.6	10.2	11.0
NE _L (MJ/kg of DM)	1,110	6.7	0.4	6.5	7.0
RDP (g/kg of DM)	1,110	110	18	99	119
RUP (g/kg of DM)	1,110	60	13	52	68
MP (g/kg of DM)	1,110	99	12	92	106

¹Nt = number of treatment means; EE = ether extract; DE = digestible energy; Q1 splits off the lowest 25% of data from the highest 75%, and Q3 splits off the highest 25% of data from the lowest 75%.

found. A potential explanation for that difference may lie in the type of data used, as in this latter work, data from beef and dairy were used for the regression.

With respect to total NAN flows at the duodenum response, it is interesting to see that the quality of prediction was similar between the 2 systems, as observed with the slope (0.72 and 0.76 for INRA and NRC, respectively) and CCC (0.74 and 0.72, respectively). This evaluation, conducted on a large data set represented by a large diversity of diets, suggests that a similar quality of estimated MP response to dietary change is obtained when either the NRC (2001) or INRA (2018) model is used.

It is important to note that in this evaluation, the exhaustiveness of data was favored over data independence. The advantage is that the evaluation can be made on a large data set representative of the diversity characteristic of indoor dairy production systems. However, the disadvantage is that data that have been used to calibrate equations in 1 or 2 of the models may also be part of the data set used for the current evaluation.

Calculated Nutritional Values

Descriptive statistics of the nutritional values for the 1,110 different rations calculated with NRC (2001) and INRA (2018) feed evaluation systems are reported in

Table 2. The calculated chemical composition values are in close agreement with actual values reported in the publications. Figure 3 shows the overall relationship between NE_L calculated by the INRA model and NE_L calculated by the NRC model. The average NE_L values from this large data set were almost identical (6.74 and 6.73 MJ/kg of DM) for NRC and INRA, respectively, and the within-experiment slope of NE_L INRA regressed against NE_L NRC was 0.94 ($\pm$ SE 0.03). However, the R² of this relationship (all reported R² obtained by models unadjusted for effect of experiment) was 0.45, indicating quite substantial differences between systems for individual diets. These differences were not explained by DMI level (expressed relative to BW), proportion of concentrate, dietary CP, or NDF content (R² < 0.04), and were considered mostly random. The overall agreement on average dietary NE_L content is quite remarkable considering the different methods used by the 2 systems to compute the final NE_L values. For example, in INRA (2018) most of the reference forage digestibility values were obtained from sheep fed ad libitum, whereas NRC (2001) uses TDN values derived from cows fed at maintenance. These unadjusted digestible energy (DE) values (i.e., unadjusted for digestive interaction effects of both models; results not shown) were on average 4% greater when estimated with the INRA than the NRC model (13.72

vs. 13.21 MJ/kg of DM; $R^2 = 0.58$). However once adjusted for the effect of digestive interactions (NRC, 2001; INRA, 2018), DE values were closer, on average 1.5% lower for the INRA model (Table 2) with $R^2 = 0.38$. The main driver for this greater correction for INRA (11.5% lower DE vs. 6.7% lower DE in NRC) was the greater negative effect of feed intake level on digestibility modeled in INRA (2018) than in the NRC (2001; Supplemental File S7, Figure S4; <https://doi.org/10.3168/jds.2020-18286>). Finally, at the level of ME, average values estimated by the 2 systems were similar (<0.3% difference, Table 2) due to less energy losses in the form of urine and CH_4 with higher feed intake levels in the INRA model (Supplemental File S7, Figure S4; <https://doi.org/10.3168/jds.2020-18286>). The R^2 between the 2 ME values was equal to 0.48, similar to R^2 found between NE_L values.

Figure 3 shows the overall relationship between MP calculated by the INRA model and MP calculated by the NRC model. Overall, RDP, RUP, and MP average contents were 3.6% higher, 6.6% lower, and 5.0% higher, respectively, when calculated with NRC (2001) than with INRA (2018, Table 2). The R^2 for the linear regressions between RDP, RUP, and MP values calculated by the 2 feed evaluation systems were 0.72, 0.48, and 0.50, indicating closer agreement between

RDP content than RUP and MP content. This was supported by the slopes (SE in parentheses) obtained through within-experiment regression of 0.87 (0.02), 0.72 (0.02), and 0.69 (0.02) between RDP, RUP, and MP content calculated from INRA (2018) and NRC (2001). In both systems, variation in MP content was mainly due to variation in RUP content as the within-experiment slopes between MP and RUP content were 0.90 (0.01) for INRA and 0.90 (0.01) for NRC. Therefore, the relatively low correlation in MP content between the 2 systems is mainly due to poor correlation found in RUP content. In contrast to RUP, variation in RDP content was not associated with variation in RDP content as calculated by INRA (slope of -0.01), whereas a significant relationship, albeit with a slope of only 0.10 (0.01), was found between MP and RDP content calculated with the NRC model.

Milk Responses to Dietary Changes in NE_L and MP Supply

MP and NE_L Efficiency. Whereas the first part of the manuscript is an evaluation of the 2 feed evaluation systems as published in NRC (2001) and INRA (2018), this second part aimed at evaluating the quality of prediction of milk responses based on nutritional val-

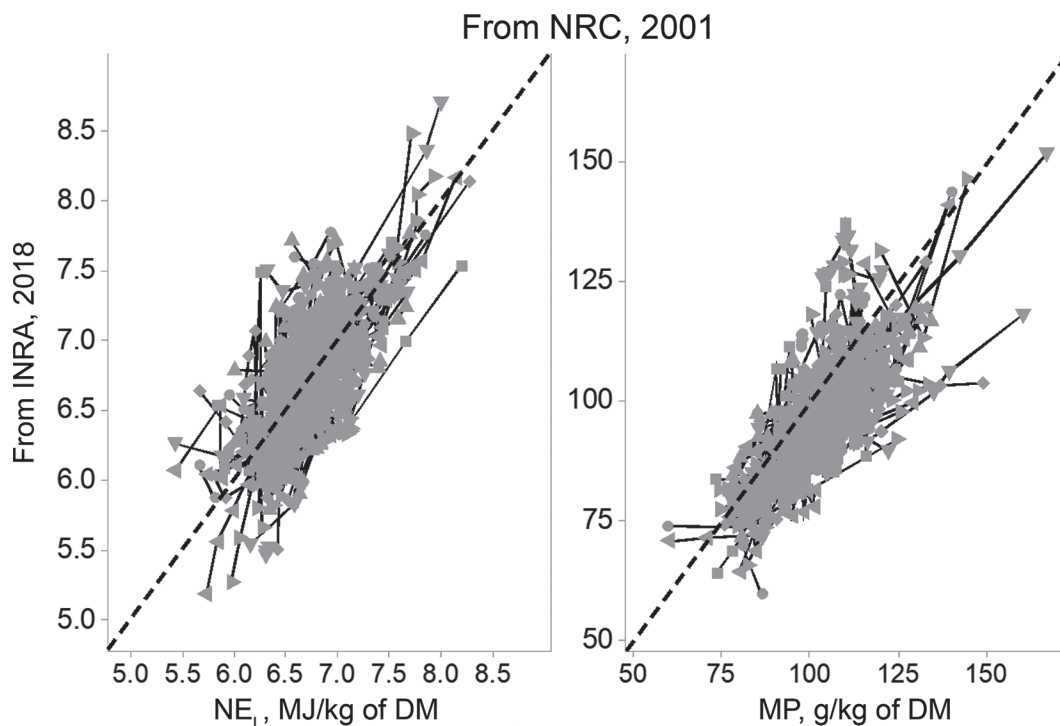


Figure 3. Overall relationships between dietary MP and NE_L contents calculated using INRA (2018) and NRC (2001). The dashed line represents the line of unity. Treatments common to an experiment are linked by a line.

ues (i.e., NE_L and MP). The intention was to develop milk response equations sensitive to changes in NE_L and MP supply for lactation specific for each system, and to evaluate how differences in estimation of NE_L and MP supply for lactation affect the estimation of milk component yields. For this some adjustments to the original NRC (2001) were made. These adjustments were for the most part related to the calculation of MP efficiency needed to express MP supply for lactation relative to a pivot supply. First, the assumption that MP efficiency is fixed (set at 67%) was dropped, and was considered variable in this paper. Indeed, there is a scientific consensus that using a variable MP efficiency improves milk protein yield prediction (e.g., Volden, 2011; Van Duinkerken et al., 2011; Arriola Apelo et al., 2014; Sauvant et al., 2020; Lapierre et al., 2018). Second, it was assumed that this variable efficiency would be used for all protein synthesis functions, which included milk protein synthesis, metabolic fecal protein losses, scurf protein synthesis, and endogenous protein efficiency. The MP requirements for all these processes were then converted into net requirements using the fixed efficiency of 67% used in the NRC (2001), and a new MP efficiency was obtained by dividing the sum of all these net protein requirements (also called total protein yield in this paper) by the total supply of MP (see Supplemental File S2, <https://doi.org/10.3168/jds.2020-18286>, for details on the calculation). This concept of using a combined but variable MP efficiency for all protein synthesis functions has been proposed in the last update of the INRA (2018) model (Sauvant et al., 2020) and was also the basis of a proposition to update MP requirement equations for the NRC model (Moraes et al., 2018). This approach differs from the first application of variable MP efficiency in feed evaluation systems (Volden, 2011; Van Duinkerken et al., 2011) where a fixed efficiency was used to estimate MP requirement for nonproductive losses and maintenance, and thus the variable efficiency was only applied to milk protein yield. These 2 approaches were compared, and it was shown that the within-experiment relationship between MP efficiency and dietary MP content had a lower RMSE (1.7 vs. 3.3% of MP efficiency) when MP efficiency was calculated with the assumption of a combined variable MP efficiency (Sauvant et al., 2015). These assumptions were already implemented in the new INRA (2018) model and were applied in this paper as well (see Supplemental File S2, <https://doi.org/10.3168/jds.2020-18286>) with the only exception that body N balance was assumed to be zero. Illustration of the variability in MP efficiency can be seen in Supplemental File S8 (Figure S5, <https://doi.org/10.3168/jds.2020-18286>). On average, MP efficiency was slightly

higher for INRA than for NRC (68.8% vs. 66.7%) and both were highly variable as indicated by standard deviation of 10.0% for INRA and 8.8% for NRC. As shown previously by others (Subnel et al., 1994; Volden, 2011; Sauvant et al., 2015) and in our data set (Supplemental File S8, Figure S5; <https://doi.org/10.3168/jds.2020-18286>), a large part of this variation was explained by the dietary MP content. With respect to NE_L efficiency, calculated as milk energy yield divided by NE_L supply above maintenance, higher values were calculated by the INRA model compared with NRC (mean $\pm$ SD, 99 ± 16 vs. $91 \pm 15\%$), leading to overall lower energy balance calculated by the former model (3.3 ± 17.8 vs. 10.5 ± 14.7 MJ/d). This difference is mainly explained by difference in NE_L maintenance requirement between the 2 systems with values 17% greater in the INRA model compared with the NRC model (0.394 vs. 0.336 MJ/kg of $BW^{0.75}$ /d).

Response Equation Calibration. The full set of equations obtained for both systems is presented in Supplemental File S4 (<https://doi.org/10.3168/jds.2020-18286>), and prediction of average milk energy and protein yields responses to changes in NE_L and MP supply for lactation are illustrated in Figure 4. In both models, MP supply for lactation expressed relative to MP pivot supply ($\Delta MP67$), curvilinearly increased milk energy yield, total protein yield and milk component yields. The regression coefficients obtained for both models were remarkably similar despite important differences in NE_L and MP value (see R^2 reported in previous part). The marginal efficiency (g of milk protein yield/g of MP for lactation) obtained with NRC decreased from 18.3%, 9.4%, to 0.6% when $\Delta MP67$ was -500 , 0 , and $+500$ g/d, respectively. Equivalent numbers for INRA were 19.2%, 9.8%, and 0.3%, respectively. These values differ from the equations derived previously on the same data set (Daniel et al., 2017), mainly because the independent variable is different. In the former analysis, all nonproductive MP requirements were subtracted from the total MP supply (i.e., fecal metabolic and scurf losses, as well as urinary endogenous losses). In the present analysis, only urinary endogenous losses, assumed to be unaffected by MP efficiency, were subtracted. This choice was made to keep MP supply for lactation independent from MP efficiency, which facilitates the application of the response equations. This inevitably results in a lower marginal protein efficiency at equivalent nutritional status. As an example, at pivot supply, the marginal protein efficiency was 19.0% in the previous analysis (Daniel et al., 2017) compared with 9.8% in the present analysis. This does not mean, however, that the expected milk protein yield response will be smaller. In

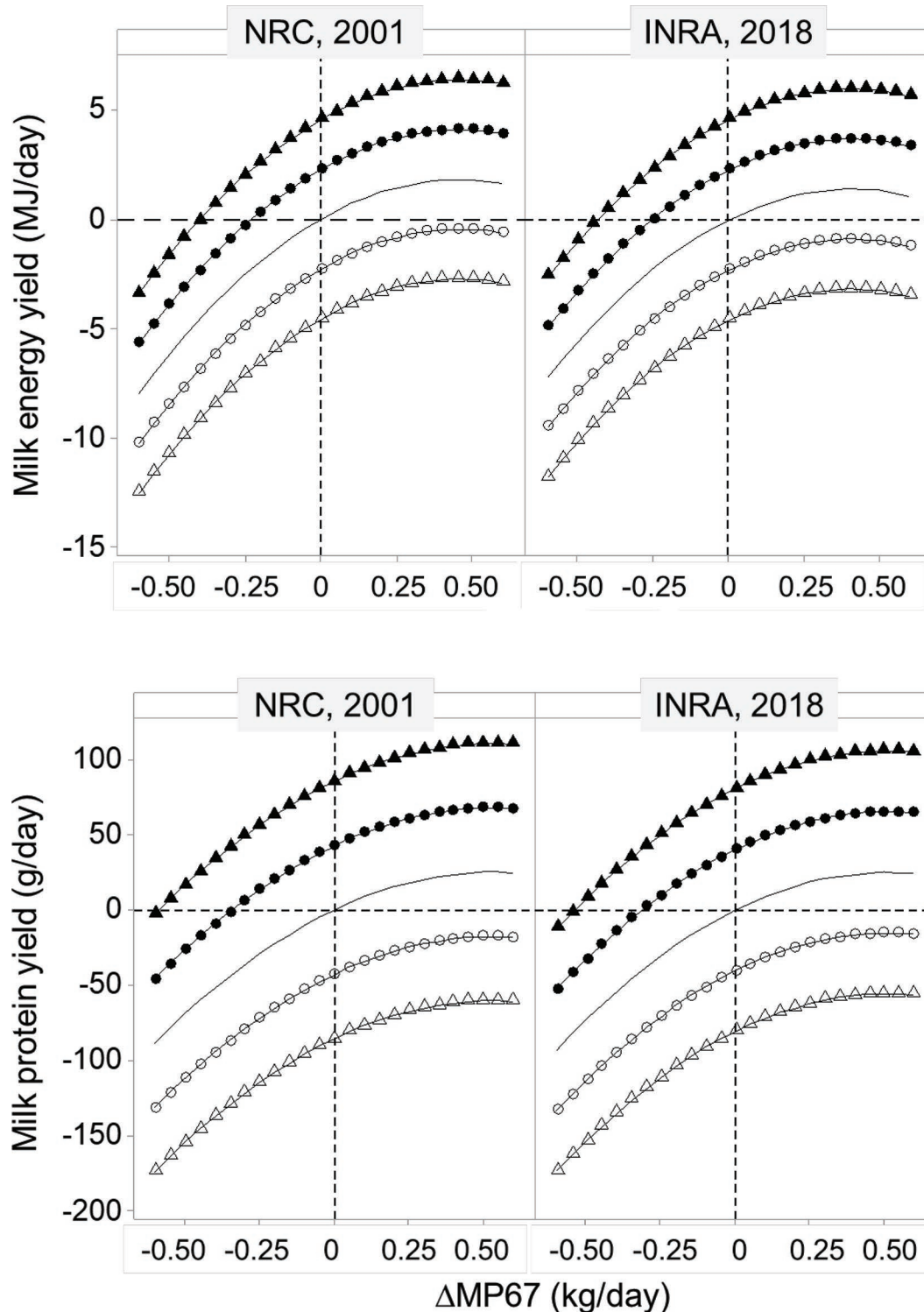


Figure 4. Prediction of average milk energy yield and milk protein yield responses to change in MP supply (g/d) and to change in NE_L supply (MJ/d) with MP or NE_L from NRC (2001) or INRA (2018). The MP and NE_L supplies are expressed relative to pivot supplies, the reference nutritional status where MP efficiency (milk protein yield/MP above maintenance) is 0.67 and NE_L efficiency (NE_L in milk/NE_L above maintenance) is 1.00. Energy effects are shown by the vertical displacement between the lines that are each for a NE_L supply relative to pivot supply: -25.0 MJ/d (solid line with Δ), -12.5 MJ/d (solid line with $\circ$), 0 MJ/d (blank solid line), +12.5 MJ/d (solid line with $\bullet$), and +25.0 MJ/d (solid line with $\blacktriangle$). Δ MP67 (kg/d) = metabolizable protein supply as calculated in Supplemental File S2 (<https://doi.org/10.3168/jds.2020-18286>), expressed relative to a MP pivot supply at which MP efficiency is 0.67.

fact, the response should be very similar. It just shows that from an increase in total MP supply, 9.8% of that MP will be partitioned into milk, whereas if expressed in terms of MP supply above maintenance, 19.0% of that MP will go into milk.

In contrast to ΔMP_{67} , the effect of ΔNE_L100 was not curvilinear but linear for all variables, except for milk lactose yield in the case of NRC. With the INRA model, an interaction between ΔNE_L100 and ΔMP_{67} supply was observed for milk lactose yield. The coefficient of 0.18 obtained in both systems for the effect of ΔNE_L100 on milk energy yield indicates that for every incremental addition of energy supply for lactation, 18% is diverted into milk. The close similarity in the shape of response curves, and thus in predicted marginal efficiency to increment in protein and energy supply, obtained using MP and NE_L values from 2 different feed evaluation systems, was striking. As DMI was used in both analyses to compute each of the dependent variables (MP and NE_L supply), a dominant role of DMI could partly explain this finding. Another reason is that, despite large differences in dietary NE_L and MP contents as calculated by the 2 models (R^2 was 0.45 and 0.50, respectively), the within-experiment slopes of 0.94 and 0.69 do not show a drastic difference in these values. The slope of 0.94 between NE_L values from the 2 models is in particular surprising considering large differences were observed in the ability of these models to predict apparent total-tract digestibility of OM (see Table 1).

It is also important to mention that due to the presence of DMI in both NE_L and MP supply, there is an inevitably high correlation between ΔNE_L100 and ΔMP_{67} (i.e., $r = 0.70$ for NRC, and $r = 0.84$ for INRA). The consequence is that the response equation can only be used with both inputs ΔNE_L100 and ΔMP_{67} , as the slope coefficient of ΔMP_{67} is influenced by the presence of ΔNE_L100 , and vice versa. Therefore, the marginal efficiencies discussed above are not independent and should be interpreted with caution.

Response Equation Evaluation. To complete the last objective of this manuscript, that is, estimating the accuracy of the 2 sets of milk response obtained, the equations were evaluated as they are intended to be used in practice. In such a scenario, we assumed milk component yields and the details of the ration fed are known, and the aim is to predict milk response to a nutritional change from this initial ration. Because of variation in production potential between cows (due to genetic but also physiological stage, and other nonnutritional environmental factors) one of the main challenges of such an application is to determine where the (group of) cow(s) is on the response curve when that initial ration

is fed. A method to solve this issue was proposed by Daniel et al. (2017) and was applied in this evaluation. Briefly, response equations obtained for milk protein yield and milk energy yield (see Supplemental File S4, <https://doi.org/10.3168/jds.2020-18286>), together with necessary inputs from the initial situation (i.e., DMI, milk component yields, and ration fed), were used to calculate the production potential. The full details of this approach are given in Supplemental File S5 (<https://doi.org/10.3168/jds.2020-18286>), and further explanation can be found in Daniel et al. (2017). In Table 3, the results of the evaluation for predicting responses in milk energy yield and milk component yields to change in MP and NE_L supply are presented. An illustration of observed responses relative to predicted responses is also shown in Figure 5 for milk component yields. It should be noted that statistics presented within Figure 5 differ from the ones presented in Table 3. In Figure 5, the slope and CCC were computed using responses predicted from initial production used (i.e., a delta of production), whereas statistics from Table 3 were done using absolute predicted yields. Independent from which statistics are used, all indicators of accuracy and precision (RMSPE, slope, CCC) were very similar between the 2 models. However, a notable difference in CCC can be found between the approach of looking at the delta of production versus the absolute predicted yield, with overall lower CCC in Figure 5 (delta of production) compared with the CCC in Table 3 (absolute yield). The lower CCC better reflects the accuracy and precision quality of response prediction, as predicted values are independent of the initial production used to calculate the pivots. The CCC is much lower for milk fat yield (0.37–0.40) than for milk protein and lactose yields (0.75–0.81), potentially indicating the limitation of only using NE_L and MP supply to predict milk fat yield response.

CONCLUSIONS

This work evaluated the ability of 2 nutritional models (NRC, 2001 and INRA, 2018) at predicting OM, NDF, and CP total-tract digestibility response, as well as response in N flows at the duodenum. Total NAN flow at the duodenum was predicted with similar accuracy and precision, but considerably better prediction was achieved when the INRA model was used to predict OM and NDF digestibility responses. The average NE_L and MP content predicted by both models was similar, but NE_L and MP content of individual diets differed substantially between both models as indicated by determination coefficients of 0.45 (NE_L content) and 0.50 (MP content). Despite these differences, this work

Table 3. Summary of observed versus predicted milk energy yield and milk component yield responses¹

Item	Model ²	N	Observed ³	Predicted ³	RMSPE ⁴ (%)	ECT ⁵ (%)	ER ⁶ (%)	ED ⁷ (%)	r ⁸	C _b ⁹	CCC ¹⁰	Slope ¹¹ (SE)
Milk energy yield (MJ/d)	NRC	543	93.1 ± 18.6	93.3 ± 19.4	5.5	0.3	7.4	92.3	0.96	1.00	0.96	0.93 (0.011)
	INRA			93.2 ± 19.4	5.5	0.1	7.9	92.0	0.96	1.00	0.96	0.93 (0.011)
Milk fat yield (g/d)	NRC	543	1,135 ± 239	1,136 ± 250	7.7	0.0	8.7	91.3	0.94	1.00	0.94	0.89 (0.015)
	INRA			1,135 ± 252	7.9	0.0	9.9	90.1	0.93	1.00	0.93	0.89 (0.015)
Milk protein yield (g/d)	NRC	543	973 ± 198	979 ± 203	6.1	1.2	5.4	93.3	0.96	1.00	0.96	0.93 (0.012)
	INRA			976 ± 204	5.7	0.5	5.9	93.6	0.96	1.00	0.96	0.93 (0.011)
Milk lactose yield (g/d)	NRC	367	1,484 ± 341	1,498 ± 340	5.8	2.6	1.3	96.1	0.97	1.00	0.97	0.97 (0.014)
	INRA			1,494 ± 343	5.8	1.4	2.4	96.2	0.97	1.00	0.97	0.96 (0.013)

¹Predicted values for treatments within an experiment were based on one randomly selected treatment from that experiment using MP and NE_L supply as inputs. One treatment from each experiment (n = 282, except for milk lactose yield where n = 178), randomly selected, was used to calculate the pivots. For each experiment, the pivots together with the respective response equations were used to predict milk energy yield and milk component yields from the other treatments. The treatments used for the calculation of the pivot were removed for the evaluation analysis.

²NRC (2001) and INRA (2018).

³Mean ± SD.

⁴Root mean square prediction error expressed as a percentage of the observed mean.

⁵Error due to intercept bias, as a percentage of total RMSPE.

⁶Error due to slope bias, as a percentage of total RMSPE.

⁷Error due to disturbance, as a percentage of total RMSPE.

⁸Pearson correlation coefficient, which gives a measure of precision.

⁹Bias correction factor, which gives a measure of accuracy.

¹⁰Concordance correlation coefficient (scale from -1 to 1); CCC = $r \times C_b$.

¹¹Slope of predicted versus observed regression as determined in PROC REG (SAS Institute Inc., Cary, NC). All slope coefficients were different from 1 ($P < 0.05$).

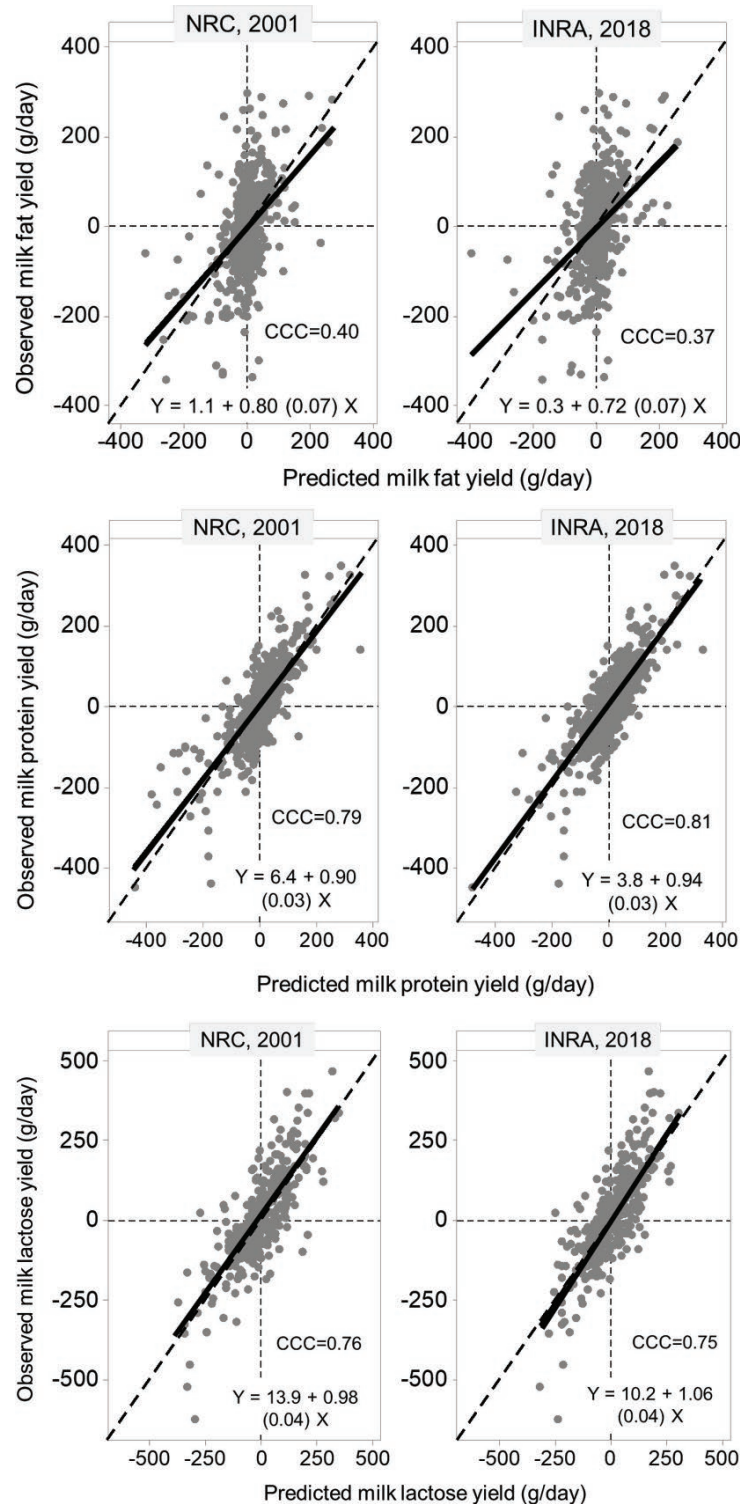


Figure 5. Comparison between observed responses of milk component yields and predicted responses. A total of 282 experiments (825 treatment means) for milk fat yield and milk protein yield, and 178 experiments (545 treatment means) for milk lactose yield, were used. One treatment from each experiment was randomly selected and used as a starting point to calculate the pivots. The response equations based on NE_L and MP supply above maintenance from either NRC (2001) or INRA (2018) were then used with these pivots to predict the milk component yields of the other treatments (543 treatments for milk fat yield and milk protein yield, 367 treatment means for milk lactose yield). The concordance correlation coefficient (CCC) and the slope displayed in the figure were not computed with absolute yields but with delta from pivot instead, and therefore differ from the slope and CCC displayed in Table 3. The dashed line represents the line of unity; the solid line represents the regression line. The SE of the slope is shown in parentheses.

shows that when response equations are calibrated with NE_L and MP values from either the INRA model or from the NRC model, the accuracy and precision of the predicted milk component yields response is similar between the models.

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